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蝶と蛾 *Tyô to Ga*, **42** (1) : 17－36, 1991

Notes on the Phylogeny and Biogeography of *Ornithoptera* BOISDUVAL (Lepidoptera : Papilionidae)

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Abstract The phylogeny and biogeography of the 13 species of *Ornithoptera* BOISDUVAL are discussed. *O. goliath* OBELTHÜR is transferred to the *tithonus* group, whilst *O. aesacus* (NEY) is transferred to the *victoriae* group. The hypothesis that *O. rothschildi* KENRICK evolved from hybridization between ancestral *O. tithonus* de HAAN and *O. chimaera* (ROTHSCHILD) is discussed. *O. euphorion* (GRAY) and *O. richmondia* (GRAY) are suggested to be more closely related to *O. croesus* WALLACE than to *O. priamus* (LINNAEUS). The combinations *O. paradisea arfakensis* (JOICEY & NOAKES) and *O. paradisea tarunggarensis* (JOICEY & TALBOT) are maintained. *O. akakeae* KOBAYASHI & KOIWAYA is suggested to be a hybrid *priamus* × *tithonus*, not *priamus* × *rothschildi* as previously recorded. Other cases of interspecific hybridization are discussed, and notes on the species are included.

Key words *Ornithoptera*, phylogeny, biogeography, interspecific hybridization, hybrid speciation, New Guinea region.

Introduction

Ornithoptera BOISDUVAL contains 13 species and some 55 subspecies or local forms. It occurs from the Moluccas, throughout New Guinea, to the Solomon Islands and eastern Australia. Taxonomically, it is best regarded as a subgenus (HANCOCK, 1983a) or synonym (MILLER, 1987) of *Troides* HÜBNER. However, in most of the recent literature it is treated as a genus and in order to minimize confusion that arrangement is followed here. The widely used subdivisions *Schoenbergia* PAGENSTECHER and *Ornithoptera* (including *Aetheoptera* RIPPON) are recognized as sections to facilitate discussion ; they are not accorded subgeneric rank. Four species-groups are recognized : *victoriae* and *priamus* groups in section *Ornithoptera*, *paradisea* and *tithonus* groups in section *Schoenbergia*. *O. goliath* OBERTHÜR, formerly considered to comprise a separate group, is referred to the *tithonus* group for reasons detailed below.

The first attempt at a phylogenetic reconstruction of the species was by ZEUNER (1943) in a pioneering study that incorporated geological data and adequately demonstrated the monophyly of the genus and sections. Further considerations on phylogeny in section *Ornithoptera* were given by SCHMID (1970) and BLANDIN (1973), but both these authors regarded *O. allottei* ROTHSCHILD as a valid species, whilst it is now accepted as a hybrid. Further notes on phylogeny were provided by HAUGUM and LOW (1978－79).

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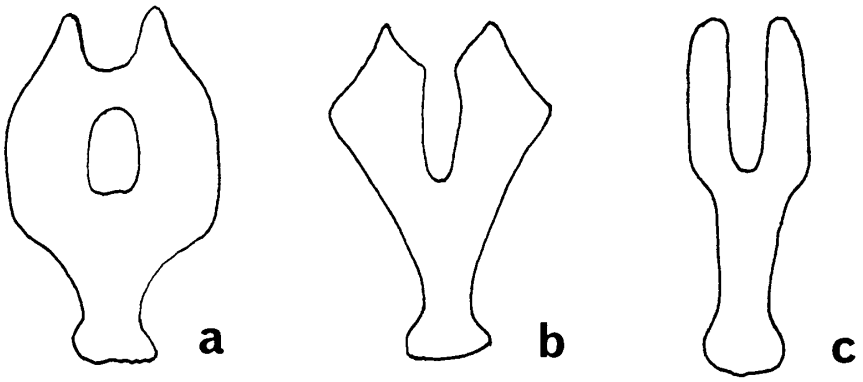

Fig. 1. The juxta in a : *Trogonoptera*, b : *Ornithoptera*, c : *Troides* (and *Ripponia*).

Opinions vary as to the relationship between *Ornithoptera* and the other birdwing butterfly genera *Trogonoptera* RIPPON and *Troides* (including *Ripponia* HAUGUM & LOW). ZEUNER (1943), HAUGUM and LOW (1978－79) and other authors regarded *Trogonoptera* and *Troides* as sister-groups but HANCOCK (1983a) and MILLER (1987) regarded *Trogonoptera* as ancestral to the sister-groups *Troides* (+ *Ripponia)* and *Ornithoptera*. This latter arrangement is supported by the deeply emarginate juxta in the male genitalia (Fig. 1), the presence of golden-yellow scaling on the hindwing, and by the similarities in abdominal colour and the structure of the male harpe in *Troides* and *Ornithoptera*, very different from the condition seen in other troidine genera, including *Trogonoptera*.

This rearrangement of the genera necessitates a reevaluation of the phylogeny of *Ornithoptera*, since it affects the interpretation of the character states shown by the various species. New information published since ZEUNER's (1943) study, particularly on early stages, geographical distributions and morphological variation, helps resolve some of the specific relationships, particularly those of *O. goliath* and *O. rothschildi* KENRICK. The present study also supports the recognition of both *O. euphorion* (GRAY) and *O. richmondia* (GRAY) as separate species, suggesting a closer affinity with *O. croesus* WALLACE than with *O. priamus* (LINNAEUS).

Notes on the 13 species and their hybrids are provided below, followed by discussions on their phylogeny and biogeography. Systematic treatments and coloured illustrations of the species were provided by D'ABRERA (1971, 1975), HAUGUM and LOW (1978－79), OHYA (1983) and SUMIYOSHI (1989).

Genus *Ornithoptera* BOISDUVAL
Section *Schoenbergia* PAGENSTECHER
paradisea group

1. *O. paradisea* STAUDINGER

This polytypic species has six described subspecies, all confined to the mainland of New Guinea. Two of the subspecies, *O. p. arfakensis* (JOICEY & NOAKES) and *O. p. tarunggarensis* (JOICEY & TALBOT), from the Arfak and Weyland Mts respectively, have black femora and females with a pale area in the hindwing discal cell, approach-

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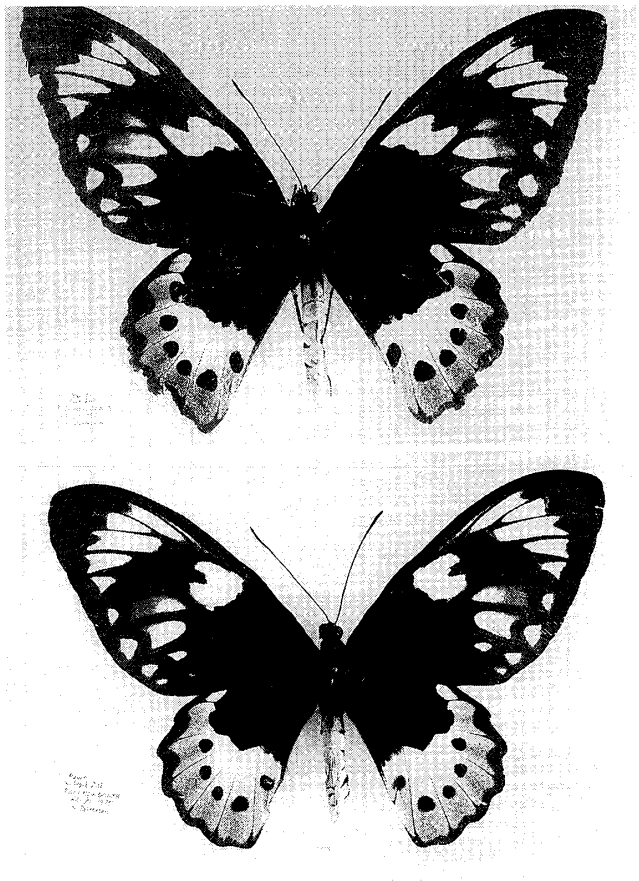

Fig. 2. Females of *O. paradisea borchi* from Ravit, West Sepik district, Papua New Guinea, showing phenotypic extremes (Specimens in Natural History Museum, Bulawayo, Zimbabwe).

ing *O. meridionalis* (ROTHSCHILD) in these characters. All other subspecies have yellow-streaked femora and a dark hindwing cell (HAUGUM and LOW, 1978－79 ; KOBAYASHI and KOIWAYA, 1979). SUMIYOSHI (1989) raised *arfakensis* to species rank but further investigation is needed before this can be accepted ; morphological differences are slight and higher altitude subspecies also occur in *O. priamus*.

The name *tarunggarensis* was applied originally to supposed females of *O. meridionalis* but HANCOCK (1982) transferred this name to *O. paradisea* on the grounds that only one species, with a *paradisea*-like male, appeared to be present in the Weyland Mts. DARBY (1985) disputed this on the basis of the *meridionalis*-like female genitalia. However, no comparison was made with the *paradisea*-like females known from the same area and there is still no evidence that more than one species is involved. The female genitalia of *O. p. arfakensis* also differ from those of the other subspecies (DARBY, 1985). PASTERNAK (1986) further discussed the taxon and suggested that two forms of it (known from one specimen of each) might occur in the Weyland Mts area, that is together with a morphologically similar form of *O. paradisea*. This is unlikely. The type specimens of *O. p. tarunggarensis* have, on the hindwing, a narrow dark marginal band and an isolated pale spot in space 7, characters typical of

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all *O. paradisea* populations except *O. p. arfakensis*. In *O. meridionalis* the hindwing marginal band is broader and the pale spot in space 7 is joined to the postdiscal band. PASTERNAK (1986) also noted that the original *O. p. tarunggarensis* specimens differ from all available *O. meridionalis* specimens from Irian Jaya. Wing shape has been used to separate *O. paradisea* and *O. meridionalis* females (HAUGUM and LOW, 1978–79) but, as shown in Fig. 2, specimens of *O. paradisea* collected at the same locality on the same day may vary considerably in wing shape. Despite this variation, typical *O. meridionalis* females have broader hindwings.

2. *O. meridionalis* (ROTHSCHILD)

This monotypic species has a disjunct distribution in southern Irian Jaya and Papua New Guinea. Western populations illustrated and discussed by PASTERNAK (1981, 1986) and KOBAYASHI (1981) are morphologically very similar to eastern populations, and differ from *O. paradisea tarunggarensis* in characters discussed above and by HANCOCK (1982). In areas of apparent overlap between this species and *O. paradisea*, females of the latter may be recognized by the yellow femora and entirely dark hindwing cell. Higher altitude (700 m) specimens from Irian Jaya are smaller and the males have more extensive forewing green areas than specimens from sea-level (PASTERNAK, 1986) and may represent a local form.

tithonus group

3. *O. goliath* OBERTHÜR

This polytypic species has four described subspecies in New Guinea (including Waigeo), plus the distinctive *O. g. procus* (ROTHSCHILD) in Ceram. An isolated population in SW Irian Jaya has females resembling those of *O. chimaera* (ROTHSCHILD) ; this will be discussed below. Usually placed in a separate group, the phylogenetic analysis presented below suggests a close affinity with *O. chimaera*, and therefore it is transferred to the *tithonus* group. The valid date of publication is OBERTHÜR (1894); the 1888 date usually adopted refers to an infrasubspecific usage (an aberration : OBERTHÜR, 1888).

4. *O. chimaera* (ROTHSCHILD)

This polytypic species, with four described subspecies and a possible local form (or additional subspecies), occurs from central Irian Jaya to Papua New Guinea, at higher altitudes than *O. tithonus* de HAAN with the two species not known to occur together. The female is characterized by rings of black hair on the abdomen, a character also seen in *O. rothschildi*. *O. c. draceana* (JOICEY & TALBOT) from the Wandamen and west Weyland Mts appears to be distinct from *O. c. charybdis* van EECKE from the east Weyland and Snow Mts, particularly in the male. *O. c. draceana* f. *sanguifluens* was described by ROUSSEAU-DECELLE (1935) from Anggi lakes, Arfak Mts. Although this was regarded as a locality error by HAUGUM and LOW (1978–79) and PARROTT and DESLISLE (1986), it may have come from a relict population nearby, as in the case of *O. tithonus misresiana* f. *ichwani*. The forewing of f. *sanguifluens*, with reduced green areas, was figured by PARROTT and DESLISLE (1986); it is distinctive and not readily

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referrable to any of the other subspecies, as shown by its referral to *O. c. charybdis* by HAUGUM and LOW (1978－79) and to typical *O. c. chimaera* by PARROTT and DESLISLE (1986). The locality data may be more accurate than has been supposed, especially as the taxon appears closest to *O. c. draceana*. SUMIYOSHI (1989) listed without comment further specimens (under *O. c. charybdis*) from the Anggi Lakes region.

5. *O. rothschildi* KENRICK

This monotypic species is confined to the Arfak Mts region of Irian Jaya. It shows a peculiar distribution of characters and its relationship to other species has been a source of much disagreement. For a useful discussion see HAUGUM and LOW (1978－79). It will be discussed further below. Like *O. chimaera*, this is a high altitude species, generally occurring above 1000 m.

6. *O. tithonus* de HAAN

This is another polytypic species with five described subspecies and one local form, probably of subspecific status. The species is confined to Irian Jaya, including the islands of Waigeo and Misool (DESLISLE, 1985, 1989). Mainland subspecies are not well differentiated and are sometimes regarded as synonyms. *O. t. misresiana* f. *ichwani* was described by KOBAYASHI and KOIWAYA (1980) from a separate mountain range in the Arfak Mts to that where typical *O. t. misresiana* (JOICEY & NOAKES) occurs.

Section *Ornithoptera* BOISDUVAL

victoriae group

7. *O. aesacus* (NEY)

This monotypic species occurs on the island of Obi, central Moluccas. In characters of the male wing colour and genitalia, particularly the harpe, it belongs in the *victoriae* group, whilst in general appearance it is similar to *O. priamus*. Usually included in the *priamus* group, it appears to be closer phylogenetically to *O. alexandrae* (ROTHSCHILD) and *O. victoriae* (GRAY) and accordingly is transferred to the *victoriae* group.

8. *O. alexandrae* (ROTHSCHILD)

This monotypic species is the largest in the genus. It is restricted to the Popondetta region of Papua New Guinea and is listed as an endangered species by COLLINS and MORRIS (1985).

9. *O. victoriae* (GRAY)

This polytypic species, with seven recognized subspecies, occurs in the Solomon Islands and Bougainville. CALDERARA (1984) showed that records of *O. v. resplendens* EHRMANN (a synonym of *O. v. regis* (ROTHSCHILD)) from Choiseul were likely to be either erroneous or vagrants, as the endemic *O. v. archeri* CALDERARA is now known to be present.

priamus group

10. *O. priamus* (LINNAEUS)

This polytypic species occurs throughout New Guinea and the Solomon Islands (except San Cristobal), including associated islands, the southern Moluccas and north-

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ern Queensland, Australia. Up to 18 subspecies are recognizable, some of which may better be regarded as local forms (HAUGUM and LOW, 1978－79 ; PARROTT, 1985, 1988, 1990). The blue subspecies *O. p. caelestis* (ROTHSCHILD) and *O. p. urvilliana* (GUÉRIN-MÉNEVILLE), from the Louisiade Archipelago and Solomon Islands－New Ireland respectively, were regarded as separate species by D' ABRERA (1975) but this has not been accepted by later workers, particularly since the latter taxon hybridizes freely with *O. p. poseidon* DOUBLEDAY (STRAATMAN, 1976). SCHMID (1973) suggested that *O. p. miokensis* RIBBE resulted from hybridization betwen *O. p. bornemanni* PAGENSTECHER *and O. p. urvilliana*, a hypothesis accepted here, particularly in the light of observations on the *poseidon* × *urvilliana* hybrids discussed by STRAATMAN (1976). Higher altitude subspecies *O. p. aureus* PARROTT and *O. p. sterrensis* PARROTT occur in the Arfak and Weyland Mts respectively (PARROTT, 1988, 1990).

11. *O. euphorion* (GRAY)

This monotypic species occurs from Cooktown to Mackay in NE Australia. Generally placed as a subspecies of *O. priamus*, it was regarded as a separate species by HANCOCK (1983a), largely on the basis of a closer affinity with *O. richmondia* than with *O. priamus*.

12. *O. richmondia* (GRAY)

This is another monotypic species often included as a subspecies of *O. priamus*. It is restricted to S. Qld and N. NSW, eastern Australia. As noted below, both this species and *O. euphorion* appear to be more closely related to *O. croesus* than to *O. priamus*, especially with regard to the shortened forewing submarginal band, the underside pattern on the hindwing and the male genitalia.

13. *O. croesus* WALLACE

Three subspecies of this polytypic species occur in the northern Moluccas (PARROTT and SCHMID, 1984), whilst a fourth, *O. c. sananaensis* TSUKADA, is known from a single female from Sanana I., southern Sula Is. When exposed to light over a long period, the orange areas turn dull green in preserved specimens.

Interspecific hybrids

Several cases of natural hybridization in *Ornithoptera* have been reported. Hybrids have been produced artificially between *O. euphorion* / *O. richmondia* and *O. euphorion* / *O. priamus macalpinei* MOULDS, resulting in progeny that are either sterile or have reduced fertility, but full details have not yet been published. Other known or suspected hybrids are discussed below, including a case involving *Troides oblongomaculatus papuensis* (WALLACE).

1. *Troides oblongomaculatus papuensis* (♂) × *O. priamus poseidon* (♀)

Male hybrids have been produced from both artificially and naturally mated examples of this combination (STRAATMAN, 1976 ; SANDS and SAWYER, 1977). Matings between the reciprocal combination have been observed but no hybrids produced (STRAATMAN, 1976). The hybrids most resemble the male parent but a number of male characters are derived also from the female parent. As noted by the preceding authors,

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these specimens demonstrate the extent to which species of *Ornithoptera* are able to hybridize under natural conditions. However, such hybridization, at least in this case, appears to be between old, worn males and newly emerged females (STRAATMAN, 1976).

2. *O. priamus urvilliana* (♂) × *O. victoriae* (♀)
(=*allottei* (ROTHSCHILD))

O. allottei was long considered to be a valid species, despite the suggestion by its original discoverer, Abbe ALLOTTE, that it was a hybrid. SCHMID (1970, 1973) and D' ABRERA (1971, 1975) particularly supported its validity as a species and the former attempted to place it phylogenetically. Other authors (ROUSSEAU-DECELLE, 1930 ; MCALPINE, 1970 ; HAUGUM and LOW, 1978－79 ; HANCOCK, 1983a) have, however, accepted its hybrid status and there can now be no doubt that it represents an *urvilliana* ♂ × *victoriae* ♀ cross. Natural matings of the above combination have been reported from Bougainville (HAUGUM and LOW, 1978－79).

Specimens have been recorded from Buin and Malaita : the subspecies of *victoriae* involved would therefore be *v. regis* and *v. reginae* SALVIN respectively. The hybrids show intermediate character states, including wing shape, between the two parent species. Both sexes are known and lack red patches on the thorax, a character shared with *O. victoriae*.

3. *O. euphorion* (♂) × *O. victoriae* (♀)

Matings between caged examples of old, worn *euphorion* males and fresh *victoriae* females have been observed recently (R. STRAATMAN, personal communication ; HAUGUM, 1990). Out of 22 eggs laid, 5 produced larvae resembling those of *O. euphorion*. Both male and female adults were produced. Males resemble specimens of *allottei* but are a golden-yellow colour above and below, and the underside of the hindwing has the black cell border and postdiscal spots better developed. The female also resembles *allottei* but the abdomen is darker, the forewing pale areas are white, the hindwing pale areas are white anteriorly and ochraceous posteriorly, and the hindwing marginal band is broader. As in *allottei* both sexes lack red patches on the thorax.

4. *O. priamus poseidon* (♂) × *O. paradisea borchi* HAUGUM & LOW (♀)

HAUGUM and LOW (1978-79) record natural matings of the above combination in the Sepik district of Papua New Guinea, but no hybrids have been recorded. The reciprocal cross apparently has not been observed.

5. *O. priamus aureus* × *O. tithonus misresiana*
(=*akakeae* KOBAYASHI & KOIWAYA)

O. akakeae was described from one male from a mountain near Anggi Lakes in the Arfak Mts, at an altitude of 2500 m, by KOBAYASHI and KOIWAYA (1978). This is the same locality from which *O. tithonus misresiana* f. *ichwani* was described subsequently (KOBAYASHI and KOIWAYA, 1980). HAUGUM and LOW (1978－79) considered it to be a hybrid between *O. priamus* and *O. rothschildi*, but there is no firm evidence that the later taxon occurs at this locality. Closer examination of *akakeae* also suggests that *O. tithonus* and *O. priamus aureus* are the parent species. Apart from the *"rothschildi"*

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characters quoted by HAUGUM and LOW (1978-79), which apply equally well to *tithonus*, the hindwing with its narrow marginal band, lack of a yellow spot in space 2, and lack of a distinct anal black patch on the underside (a few scattered scales are present, fewer than in *tithonus* but more than in *aureus*), and the underside of the forewing with an entire green patch in space 6 (green or with a very few black scales centrally in *tithonus* and *aureus*, with a distinct black central patch in *rothschildi*), all suggest that *O. tithonus misresiana* f. *ichwani* is one of the parents.

Further male specimens of *akakeae* were reported by HAUGUM and LOW (1981) from the Arfak Mts. Their illustrated specimen differs from typical *akakeae* in the better developed apical portion of the forewing green radial band, a more elongated hindwing, and fewer yellow submarginal hindwing spots. This specimen differs from typical *akakeae* in the same manner that *tithonus misresiana* differs from f. *ichwani*, lending further support to the *tithonus* × *aureus* hypothesis. The *akakeae* specimens recorded by HAUGUM and LOW (1981) are likely to be the result of crosses between *O. priamus aureus* and *O. tithonus misresiana*.

An interesting feature of these specimens is the appearance of *"rothschildi"* characteristics in a hybrid involving *tithonus*.

6. *O. goliath* × *O. tithonus*

PORTENEUVE and BLANDIN (1980) discussed and illustrated a male specimen from near Fak Fak, Onin Peninsula, that appears to be a hybrid between *O. goliath atlas* (ROTHSCHILD) and *O. tithonus tithonus*. The forewing has the cubital band separated from the anal one and, on the underside, no central black patch in the green area in space 6, space 1a black and space 1b entirely green. As in *goliath*, the hindwing has extensive yellow areas.

This taxon was also discussed and illustrated by HAUGUM and LOW (1981), together with another male specimen from the Arfak Mts. This latter specimen has better developed green areas on the hindwing and smaller radial and cubital green bands on the forewing, and appears to be a hybrid between *O. goliath samson* NIEPELT and *O. tithonus misresiana*.

Again, it is interesting to note the appearance of *"rothschildi"* characteristics, mentioned by HAUGUM and LOW (1981) in a hybrid involving *tithonus*.

7. *O. goliath samson* × *O. rothschildi*

RIO (1982) illustrated and discussed a male from the Arfak Mts that appears intermediate between *O. goliath* and *O. rothschildi*. Unlike the *goliath* × *tithonus* hybrids, the forewing green cubital band is distinctly joined to the anal band (at most only a trace of green scales in *goliath* × *tithonus* hybrids), and the hindwing space 2 is green with a large yellow spot at each end (narrowly green with only a basal yellow spot in *goliath* × *tithonus* hybrids). On the underside, the forewing has space 1a black, 1b green and the green area in space 6 with a black central spot, whilst the hindwing has the cell narrowly margined with black and no black spot in space 1b.

8. *O. goliath atlas* × *O. chimaera charybdis*

STRAATMAN (1979) discussed an unusual population of *goliath* and *chimaera* from isolated plateau near Wamena in the Central Highlands of Irian Jaya, at an altitude of

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1900－2500 m. Adults and larvae of these two species show convergences in pattern, suggested by STRAATMAN (1979) to be the result of mimicry. The most striking feature is the presence of rings of hair on the abdomens of the *goliath* females, similar to those seen in *O. chimaera*. Whilst the abdominal and wing pattern convergences could be the result of mimicry, it seems unlikely that this would be the case with the rings of hair.

A number of colour photographs of both species from this locality have been examined. These, together with the notes provided by STRAATMAN (1979), suggest that genetic introgression has taken place between the two species. Apart from the hairy female abdomens noted above, *goliath* larvae from this population have the pale abdominal 'saddle' reduced, but still larger than the reduced condition seen in typical *chimaera* (STRAATMAN and SCHMID, 1975), whilst those of *chimaera* from this locality are darker than the typical form. Females of both species from this locality vary considerably in pattern, with white cell patches on both wings present or absent.

The presence of this population, with its characters indicating genetic introgression rather than mimicry, suggests that *goliath* and *chimaera* are more closely allied than has generally been supposed. If they were distantly related (*e. g.* in different species-groups), then isolated hybrids between the two species would be expected but the two taxa would remain as distinct from each other as in other populations. There are several morphological characters which also suggest a close relationship. In the males, these include the broad wing, forewing pattern, particularly the joining of the cubital and anal green bands and, on the underside, the almost entirely green coloration (apart from the postdiscal spots), and the hindwing pattern, with the extensive yellow areas and only three postdiscal dark spots (rarely 4), which are placed further from the cell than in related species. In the female, the underside of the hindwing has the black border narrow and with a sinuous inner edge. In related species this border has an inner edge that may be deeply indented but is not noticeably sinuous.

Since both species have managed to maintain their specific identities in this population, it is likely that hybridization occurs on a limited scale. It may also be one-sided, since most of the morphological changes appear to have occurred in *goliath*. For example, hybridization between worn *goliath* males and newly-emerged *chimaera* females, followed by backcrossing, would enable *chimaera* characters to enter the *goliath* population, whilst failure of the reciprocal cross would ensure the maintainance of a normal *chimaera* population.

Similar cases of genetic introgression have been reported in North American Papilionidae, notably in *Pterourus glaucus* × *P. rutulus* (BROWER, 1959 ; SCOTT and SHEPPARD, 1976) and the *Papilio machaon* group (FISHER, 1977 ; FERRIS and EMMEL, 1982).

Ornithoptera rothschildi

There is no doubt amongst authors that *O. rothschildi* belongs in the *tithonus* group but there has been much disagreement over its relationship to other members of the group, viz. *tithonus*, *chimaera* and *goliath*. HAUGUM and LOW (1978－79) discussed

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the problem in depth and surmised that *rothschildi* should be placed phylogenetically between *goliath* and *chimaera* / *tithonus*. However, the placing of *goliath* as a close ally of *chimaera*, and the recognition of *tithonus*, not *rothschildi*, as one of the parents of the hybrid *akakeae*, have a profound effect on the arguments they used. This is particularly true with regard to the suggestion by HANCOCK (1978, 1983a) and in HAUGUM and LOW (1978－79) that *rothschildi* evolved as a result of hybridization between ancestral *tithonus* and *chimaera*, developing into a species in its own right through subsequent isolation.

HAUGUM and LOW's (1978－79) phylogeny is the most acceptable of conventional arrangements but still does not satisfactorily explain the numerous character convergences seen with *chimaera* or *tithonus*, nor the absence of certain characters shared by *goliath* and *chimaera*. Apart from its occurrence at similarly high altitudes, *rothschildi* shares with *chimaera* the following characters : In the male ; the narrow connection of the green cubital and anal bands on the forewing, the large black spot in space 1b on the underside of the hindwing, the reduced hindwing tornal angle. In the female ; wings with distinct white fringe spots, abdomen with rings of black hair. The following characters are shared with *tithonus* : In the male ; the dark cell apex and space 1a on the underside of the forewing, the green postdiscal band on the hindwing, especially on the underside, which also has a row of, generally, 5 or more postdiscal black spots, a black patch often present at the cell apex, a black border to the lower part of the cell, no yellow patch at the base of space 2 but a yellow patch present submarginally (only in some *tithonus*, notably in f. *ichwani*). In the female ; the broader, irregularly indented border on the underside of the hindwing. Features common to both *chimaera* and *goliath*, but lacking in *rothschildi*, include : In the male ; the broad wings, particularly the forewing with its well developed tornal angle, the largely green cell on the underside of the forewing, the enlarged yellow areas on the hindwing, with the postdiscal black spots reduced to (generally) 3 and situated well away from the cell, and a yellow area at the base of space 2. In the female ; the narrow sinuous black border on the underside of the hindwing.

Although some specimens of *tithonus* and *goliath* from the Arfak Mts have ventral hairs on the abdomen in females, the distinct rings of hair are seen only in *chimaera* and *rothschildi* (and in the introgressive *goliath* population discussed above). Convergence in both this character and the wing fringe spots in females is unlikely, as both appear to be specializations in *Schoenbergia*. Subsequent loss of these characters in *tithonus* and *goliath*, if they are ancestral, is unlikely since the hairy abdomen is dominant in the introgressive *goliath* population and the white wing fringe spots are indistinct or absent in all species of *Schoenbergia* except *rothschildi* and *chimaera*, particularly on the forewing, although they are narrowly present on the hindwing in *tithonus* and *goliath*.

The characters of *rothschildi* do show a number of features intermediate between *chimaera* and *tithonus*, particularly in wing shape, forewing pattern and width of hindwing space 2. Others are derivable either from *chimaera* or *tithonus*. Characters

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common to *chimaera* and *goliath* but lacking in *rothschildi* all appear to have been modified towards the condition seen in *tithonus*. Even the reduced radial green band on the forewing in males, suggested by HAUGUM and LOW (1978－79) to be a character unique to *rothschildi*, is similar to that seen in *tithonus* f. *ichwani* and *chimaera* f. *sanguifluens*, both of which possibly occur in areas neighbouring the Arfak Mts. The extended yellow submarginal spots on the hindwing, including that in space 2, is another character shared with *tithonus* f. *ichwani*.

HAUGUM and LOW (1978－79) objected to the hypothesis of speciation via hybridization in the case of *rothschildi* on the grounds that "the distinct genitalia of the *rothschildi* male are practically intermediate between *goliath* on the one hand *tithonus* on the other" and "there are a number of characters which are shared with *goliath* (or which approach the character state in *goliath*), but which are absent in both *chimaera* and *tithonus*", suggesting that this demonstrated the near impossibility of a hybrid origin. However, the recognition of *goliath* as a close ally (immediate ancestor) of *chimaera* changes all this, since an ancestral *chimaera* would be likely to retain some *goliath* characteristics, such as male genitalia and wing venation, before their subsequent modification as *chimaera* evolved.

Many of the *rothschildi* characters considered unique by HAUGUM and LOW (1978－79) may be the result of hybridization ; many also appear to be associated with a melanistic tendency. Since the species has undergone subsequent isolation, some unique characters would be expected to appear. The restricted distribution of *O. rothschildi* is also of interest, being contiguous with that shown by several other taxa at the subspecies level and with no evidence to suggest it was any more widespread in the past.

The hybridization hypothesis will be discussed further below in relation to the overall phylogenetic model for the group. The hybrids discussed in the section above, particularly those involving *tithonus*, demonstrate the possibility of *rothschildi* indeed having a hybrid origin, although there is no dispute that it now functions as a reproductively viable species in its own right. This hypothesis does away with all cases of character convergences invoked to explain the conventional arrangement noted earlier and fulfils the rule of parsimony. It will be suggested that ancestral *tithonus* and *chimaera* are likely to have coexisted in the Arfak Mts and that this locality does provide the necessary isolation required for speciation to take place once the parent populations have intermingled genetically. The presence of *O. tithonus misresiana* and f. *ichwani* in different areas of the Arfak region suggests that a dual invasion of the area by *tithonus* has occurred ; the similarities between *misresiana* and typical *tithonus* also suggest that the former is a more recent arrival than the relict f. *ichwani*.

This is not the only case of suspected speciation via hybridization in the Papilionidae. It may account also for the characters of the Sulawesian *Graphium dorcus* (de HAAN) and many of the North American "species" in the *Papilio machaon* group (HANCOCK, 1983a).

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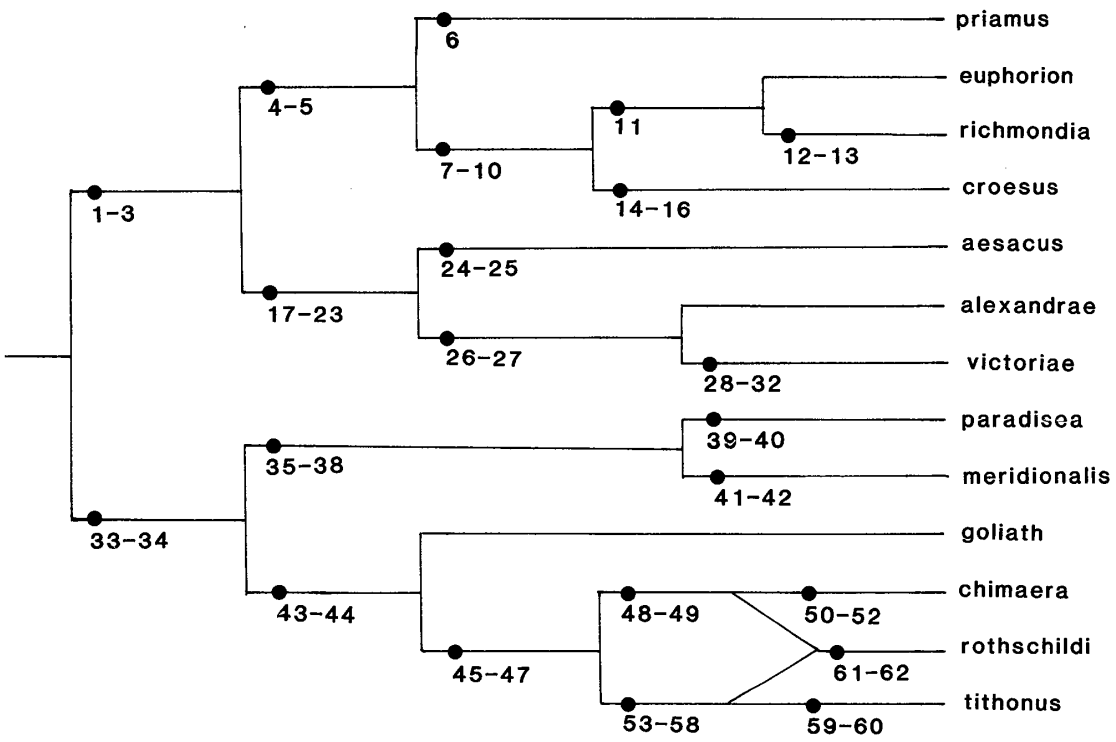

Fig. 3. Suggested phylogenetic relationships of the species of genus *Ornithoptera*. See text for explanation of character states 1 – 62.

Phylogeny and Biogeography

The proposed phylogenetic relationships of the 13 species are shown in Fig. 3, with the various derived character states employed discussed below. The following character states are presumed to be primitive, based on outgroup comparison with *Trogonoptera* and *Troides*, especially *Ripponia* (the most primitive subgenus), or their distribution within the genus *Ornithoptera*.

Male sex patch on the forewing absent ; green areas of both wings extensive ; yellow areas of hindwing submarginal ; thorax laterally red in both sexes ; male harpe relatively narrow, with irregularly placed terminal teeth and the base broad ; male hindwing not tailed, truncate, the apical angle distinct, the underside with the veins of the cell narrowly black and with submarginal spots but no distinct black spot in space 1b ; male forewing with postdiscal internervular dark spots on the underside and no large black area at apex of cell ; female with the submarginal spots of the hindwing more or less rounded and placed towards the cell, and white fringe spots of both wings indistinct ; female without abdominal rings of hair ; thorax dorsally with a medial metallic green patch, at least in males ; mature larva with a pale abdominal saddle and with the tubercles black and red ; pupa yellowish-brown.

The following derived character states are in many cases complex and do not lend

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themselves to tabulation. Some apparent cases of convergence and character reversal are evident, although in the latter case this is possibly a result of genetic introgression. Some cases of convergence are obviously polyphyletic ; for example the black thorax, which is sex-linked in *O. aesacus* but not in *O. victoriae*.

Characters 1 – 3. Section *Ornithoptera*. The male forewing has a postdiscal sex patch (1) and a reduced or absent cubital band (2). The sex-brand is absent in section *Schoenbergia* and related genera, whilst the derived nature of the cubital band was discussed by HAUGUM and LOW (1978 – 79). In females, the submarginal hindwing spots tend to be more wedge-shaped and closer to the margin than in *Schoenbergia* (3).

Characters 4 – 5. The *priamus* group. The male harpe is narrow at the base and broad apically (4), and has the basal hooks reduced (5). The polarity of these states is uncertain, but the opposite conditions are seen in the *victoriae* group and in *Schoenbergia*.

Character 6. *O. priamus*. In the female, the red thoracic hairs do not extend to the prothorax (6), this being wholly black. The male has the submarginal band of the forewing elongate, reaching almost to the wing apex, and the hindwing cell veins at most narrowly black.

Characters 7 – 10. *O. euphorion* and allies. The male has the hindwings more rounded and less truncate (7), with the cell veins broadly black (8), and the submarginal band of the forewing shortened (9). On the underside of the hindwing, the male has a distinct black spot or scales in space 1b (a character which also occurs in some subspecies of *O. priamus*), whilst the submarginal areas become golden, contrasting with the green postdiscal and discal areas (10).

Character 11. *O. euphorion* and *O. richmondia*. The pale saddle usually present on the abdomen of the mature larva is absent (11). The males retain a green iridescent wing colour.

Characters 12 – 13. *O. richmondia*. The male harpe is shortened (12) and the pupa is green (13). In *O. euphorion* the harpe is elongate and the pupa yellow-brown.

Characters 14 – 16. *O. croesus*. The mature larva has a pale abdominal saddle. The male wing colour is iridescent orange (14), whilst the yellow hindwing areas extend into the cell (15). As in *O. richmondia*, the male harpe is shortened (16); this and even further reduced submarginal forewing band suggest a close affinity with *O. richmondia* but the geographically intermediate position of *O. euphorion* renders this unlikely. The short harpe and greatly reduced submarginal band are possibly common characters of the ancestor of all three species, the more elongate conditions seen in *O. euphorion* representing reversals towards the *priamus* condition, perhaps as a result from limited introgression from *priamus* during the early phase of its evolution. The females of *O. croesus croesus* and *O. euphorion* are very similar in appearance, providing further evidence of their close relationship.

Characters 17 – 23. The *victoriae* group. The male has the forewing cell broadened (17) and the hindwing cell elongate (18), whilst the apical angle of the hindwing becomes rounded (19), less distinct than in the *priamus* group. The male harpe has the terminal teeth in a circular series (20), rather than in an irregular series, whilst the distal spines

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of the valvae become narrowed (21). The male forewing has the apex of the cell broadly black on the underside (22), whilst the hindwing becomes more or less rounded marginally (23), rather than crenulate.

Characters 24 – 25. *O. aesacus*. In the female the thorax is laterally black (24), the red being retained by the male. The male has the basal hooks of the harpe reduced (25). This latter state appears to be convergent to that seen in the *priamus* group as other characters show a close relationship with the *victoriae* group ; like *euphorion*, there may have been some introgression with *priamus* during the initial evolutionary phase.

Characters 26 – 27. *O. victoriae* and *O. alexandrae*. The male forewing becomes oval in shape (26), rather than triangular, whilst the hindwing becomes very elongate (27).

Characters 28 – 32. *O. victoriae*. The thorax is black laterally in both sexes (28). The "*allottei*" hybrids show that this condition is dominant and therefore most probably derived. It is convergent to the condition seen in *O. aesacus*, but not sex-linked as in the latter case. The male harpe has only one basal hook (29); the larva lacks the pale abdominal saddle ((30), convergent with *euphorion* and *richmondia*) ; the forewing of the male has the cubital and radial bands modified into broad patches (31); and the female pattern is modified (32). Primitive states of these characters are retained by *O. alexandrae*.

Characters 33 – 34. Section *Schoenbergia*. The male hindwing has the apical angle rounded ((33), convergent with the *victoriae* group) and the yellow basal areas joined to the submarginal areas (34), *i. e.* the yellow areas are extensive. The apical angle of the hindwing is distinct in both *Trogonoptera* and *Troides*.

Characters 35 – 38. The *paradisea* group. The male has the hindwing narrow (35) and tailed at vein 2 (36), whilst the underside lacks dark submarginal spots (37). The male also lacks submarginal dark patches on the underside of the forewing (38). This latter state is possibly primitive, the dark spots seen in subgenus *Ornithoptera* and the *tithonus* group thus being convergent ; however this is considered to be unlikely as the internervular areas remain dark in those species of *Troides* that show some pale scaling on the forewing, and also in *Trogonoptera*.

Characters 39 – 40. *O. paradisea*. The male has the tornal angle of the forewing rounded (39) and the harpe broadened dorsolaterally (40).

Characters 41 – 42. *O. meridionalis*. The male has the hindwing greatly reduced (41) and the forewing with the apex of the cell broadly black (42). This latter condition is convergent to that seen in the *victoriae* group and in *O. tithonus* / *O. rothschildi*.

Characters 43 – 44. The *tithonus* group. The male has the thorax medially black (43), without the medial green streak seen in other groups. The mature larva has black tubercles (44), rather than red and black ones.

Characters 45 – 47. *O. chimaera* and allies. The male has the hindwing narrowed (45), the radial band of the forewing narrowed along the cell (46) and the anal and cubital bands of the forewing not or only weakly connected (47). Primitive states of these characters are seen in *O. goliath*.

Characters 48 – 49. *O. chimaera* and *O. rothschildi*. The female abdomen has rings of hair (48) and the wing fringes have well developed white spots (49).

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Characters 50 – 52. *O. chimaera* alone. The male harpe has only one basal hook (50) and is broadened ventrally (51). The mature larva has the pale abdominal saddle reduced (52); this may not be a specific character as the condition in *tithonus* and *rothschildi* is unknown, and may refer to *chimaera* and allies. A pale saddle is present in *O. goliath*.

Characters 53 – 58. *O. tithonus* and *O. rothschildi*. The male hindwing has a distinct green postdiscal band (53) with the spots in spaces 3 and 4 postdiscal (54) rather than submarginal. The male forewing has the tornal angle rounded (55), whilst on the underside the cell apex is broadly black (56) and space 1a is black (57). The underside of the hindwing has a submarginal black spot in space 2 (58).

Characters 59 – 60. *O. tithonus* alone. The male has space 1b on the underside of the forewing with its lower half black (59) and space 2 on the underside of the hindwing is very narrow (60).

Characters 61 – 62. *O. rothschildi* alone. The males show a melanistic tendency (61) and the eggs are very small (62).

The following scenario for the group is proposed. The original dispersal centre of the genus appears to be the central region of the island of New Guinea, with initial separation into a lowland section *Ornithoptera* and a highland section *Schoenbergia*, with present-day *O. priamus* and *O. goliath* respectively representing the ancestral species. Several species now occupy peripheral localities such as the Moluccas, Solomon Islands and Australia.

Section *Ornithoptera* appears to have dispersed from the northern lowlands to the west, probably to the Onin Peninsula area, resulting in the development of the *victoriae* group (as *aesacus*) in the west and leaving the *priamus* group (as *priamus*) in the north. After undergoing various modifications in wing shape and colour (the iridescent green band becoming more turquoise with a violet sheen), and male genitalia, the *victoriae* group ancestor spread eastwards, to the south of the central mountains. Although *O. victoriae* retains green iridescent areas, these change to violet in preserved specimens exposed to light over a long period. Subsequent marine incursions presumably resulted in the isolation of *O. aesacus* in the west and *O. alexandrae* in the east, the latter becoming further modified after an offshoot from it reached the Solomon Islands as *O. victoriae*. This eastern representative is the most specialized of the group and, as in the case of other Papilionidae (including *O. priamus*), appears to have reached the Solomon Islands from eastern Papua New Guinea, via the Louisiade Archipelago. *O. alexandrae* is now restricted to a small area on the mainland ; some of its character states may have been modified subsequently by limited introgression with *O. priamus*. These characters were discussed by BLANDIN (1973), and commented upon by HAUGUM and LOW (1978 – 79). There is no evidence to support the suggestion by ZEUNER (1943) that a volcanic mountain chain to the north of New Guinea provided a dispersal route between the Northern Moluccas and the Solomon Islands during the Miocene. This chain had probably disappeared before any significant dispersal in *Ornithoptera* occurred. Furthermore, the Northern Moluccas do not appear to have played a part in the early stages of Papilionidae speciation and dispersal in the New Guinea region (HAN-

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COCK, 1983b), and *O. croesus* does not appear to be as primitive as ZEUNER (1943) assumed.

The *priamus* group, meanwhile, spread southwards, displacing the *victoriae* group or replacing it following marine incursions to the south of the central mountain range. Here it appears to have evolved into an *O. euphorion*-like species, with a reduced forewing submarginal green band and a black-margined hindwing cell. From here it dispersed westwards, perhaps displacing *O. aesacus* from the Onin Peninsula to the Southern Moluccas. Again displaced from southern New Guinea by marine incursions, the ancestor reached Australia and differentiated into a southern species, *O. richmondia*, and a northern species, *O. euphorion*. The western population possibly was then displaced by *O. priamus* to the Northern Moluccas, via the Arfak Peninsula, as *O. croesus*. *O. priamus* also reached the Southern Moluccas and may have then displaced *O. aesacus* to the Central Moluccan island of Obi, again possibly with some limited introgression between them. As noted by ZEUNER (1943), the Arfak Peninsular region was effectively isolated from the remainder of New Guinea during the early dispersal phases of *Ornithoptera*, thus supporting the suggestion that *O. aesacus* reached Obi via the southern route.

In the central highlands of New Guinea, section *Schoenbergia* appears to have differentiated into a western *paradisea* group and an eastern *tithonus* group. *O. paradisea* and *O. meridionalis* appear to have differentiated in the foothills to the north and south of the Weyland Mts, perhaps adapting to lower altitudes as a result of a westward encroachment of the *tithonus* group, whose members generally prefer higher altitudes. The primitive *paradisea* subspecies *arfakensis* and *tarunggarensis*, with their black femora and *meridionalis*-like females, suggest that *O. paradisea* has a western, rather than an eastern origin, the yellow-femured subspecies subsequently dispersing throughout much of New Guinea. *O. meridionalis* appears to have spread to southern Papua New Guinea relatively recently, judging by the apparent lack of subspeciation.

The *tithonus* group, represented primitively by *O. goliath*, also spread westwards, resulting in the formation of ancestral *O. chimaera* in the Weyland Mts and *O. tithonus* in the Onin Peninsula. Both of these appear to have spread to the Arfak Mts and relict populations of both may still exist there. In the Anggi Lakes region, however, these two species appear to have genetically intermingled, to produce a hybrid population now differentiated into *O. rothschildi*. The distinct subspecies *O. paradisea arfakensis* also occurs here and this appears to be an isolated locality where speciation can occur but from which there appears to be no dispersal. For it to have been possible for *O. rothschildi* to have evolved in such a manner, both ancestral *O. chimaera* and *O. tithonus* must have been capable of reaching the Arfak Mts. The presence of *O. tithonus* f. *ichwani* and (probably) *O. chimaera* f. *sanguifluens* in the area suggest that they did, at about the same time that *O. paradisea* reached there to become *O. p. arfakensis*. The presence of *O. tithonus misresiana* in the area is easily explained as this is very close to typical *O. t. tithonus* and is evidently a recent arrival. The ease by which present-day species of *Ornithoptera* hybridize and the evidence of genetic introgression in the *goliath* / *chimaera* case discussed earlier show that it would be

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theoretically possible (indeed probable) for ancestral *chimaera* and *tithonus* to mingle genetically and produce a viable population, particularly in the light of their sister-species relationship. There is no reason to suppose that hybridization did not occur with equal ease in the past, and it would be unsound to ignore the possible consequences of this on the evolutionary history of the genus. The suggestion that *chimaera* is ancestral to *tithonus* is supported by the presence of the rare *O. chimaera* f. *quinquemaculata* in the Weyland Mts (PARROTT and DESLISLE, 1986), in which the hindwing has a green postdiscal band otherwise seen only in *tithonus* and *rothschildi*. Whether independently derived or a result of introgression, this green hindwing band is evidently a derived character. Wing shape and pattern characters show that *chimaera* lies between *goliath* and *tithonus* on the evolutionary line, and that *goliath* is the most primitive. That *tithonus* evolved to the west of *chimaera* is supported by the present distributions of the two species. *O. goliath* has been able to disperse more widely and has even reached the Southern Moluccan island of Ceram.

Acknowledgements

I especially wish to thank the late R. STRAATMAN, G. SANKOWSKY and A. G. ORR for much unpublished data, particularly involving hybridization. Mr R. STRAATMAN also kindly supplied photographs of many interesting taxa, and over the years I benefitted enormously from his comments and observations on the genus. I also thank D. P. A. SANDS and J. HAUGUM for their comments on various matters, and the many authors who kindly supplied separates of their papers.

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摘　　要

トリバネアゲハ属（鱗翅目，アゲハチョウ科）の系統と生物地理（D.L. HANCOCK）

筆者は，雄交尾器の juxta (Fig. 1) や harpe の形状，腹部の色彩などからトリバネアゲハ（*Ornithoptera*）属はアカエリトリバネアゲハ（*Trogonoptera*）属よりもキシタアゲハ（*Troides*）属に近縁であり（HANCOCK, 1983a ; MILLER, 1987）キシタアゲハ属の亜属としてもよいと考えているが，ここでは混乱を避けるため一般に受け入れられているように独立の属として扱った．

本稿は ZEUNER (1943) によって提唱されたトリバネアゲハ属の系統と生物地理学的関係ならびにそれ以降の分類体系を再検討するものである．その結果，本属に 13 種を認めるとともに Fig. 3 に示した種間の系統関係が推定され，本属を以下の 2 セクション 4 種群に分割した．

Section *Schoenbergia* : *paradisea* 群（*paradisea, meridionalis*），*tithonus* 群（*goliath, chimaera, rothschildi, tithonus*）

Section *Ornithoptera* : *victoriae* 群（*aesacus, alexandrae, victoriae*），*priamus* 群（*priamus, euphorion, richmondia, croesus*）

従来の分類体系からの主な変更点等は以下のとおりである．

O. goliath は単独の種群として扱われることが多かったが，*chimaera* に最も近縁であることが推定され，*tithonus* 群に移した．また，従来 *priamus* 群に置かれていた *aesacus* を *victoriae* 群に移した．*O. euphorion*

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と *richmondia* は *priamus* の亜種とされることが多かったが，*priamus* よりも *croesus* に近縁であると考えられ独立種として扱った．また，SUMIYOSHI (1989) は西イリアンの Arfak 産の *arfakensis* を独立種としたが，形態的差異は非常に小さいので西イリアン Weyland Mts 産の *tarunggarensis* とともに *paradisea* の亜種として扱った．

本稿では，トリバネアゲハでよく報告されている雑種についての再検討も行い以下の結論を得た．

(1) *O. allottei*： ROUSSEAU-DECELLE (1930), MCALPINE (1970), HAUGUM and LOW (1978－79) などが指摘するように *allottei* は *priamus* × *victoriae* から生じた雑種である．特に HAUGUM and LOW (1978－79) はソロモン諸島の Bougainville において *O. priamus urvilliana* ♂と *O. victoriae* ♀の自然交尾個体を報告している．

(2) *O. akakeae*： HAUGUM and LOW (1978－79) は *O. akakeae* を *priamus* × *rothschildi* から生じた雑種としたが，詳細な斑紋パターンの解析から *priamus aureus* × *tithonus misresiana* f. *ichwani* から生じた雑種であるという結論に達した．

(3) *O. rothschildi*： 筆者（HANCOCK, 1978, 1983a) が提唱した「*O. rothschildi* は西イリアンの Anggi 湖付近で *chimaera* と *tithonus* の祖先種間の雑種個体群が隔離，維持されて生じた種である」という説を再度提示した．

(4) *Goliath* × *chimaera*： 西イリアンの Wamena 付近の高地では *goliath* × *chimaera* から生じた雑種と考えられる個体がえられる．これは *goliath* と *chimaera* が従来考えられていたよりも近縁であり，この地域において遺伝質浸透が起こっていることを示唆する．

(5) その他 *euphorion* × *victoriae*, *goliath* × *tithonus*, *goliath* × *rothschildi*, *priamus* × *Troides oblongomaculatus papuensis* から生じた雑種についても論じた．

本稿ではトリバネアゲハ属の種分化，分布の成立過程についても考察を加えた．トリバネアゲハ属はニューギニアの中心部を起源とし，Section *Ornithoptera* の各種の祖先種がニューギニアの低地や，マルク諸島，ソロモン諸島，オーストラリアなどの周辺域に分布を拡大する一方，Section *Schoenbergia* の祖先種の生息域はニューギニアの山岳地帯に限定されていったと考えられる．（文責　広渡俊哉）

（Accepted January 5, 1991）

Published by the Lepidopterological Society of Japan, c/o Ogata Hospital, 2-17, Imabashi 3-chome, Chuo-ku, Osaka, 541 Japan

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